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Nr. 3. Johs. Schmidt: REMARKS ON THE METAMORPHOSIS AND DISTRIBUTION OF THE LARVAE OF THE EEL (*ANGUILLA VULGARIS*, TURT.). WITH ONE PLATE AND ONE CHART

KØBENHAVN
I KOMMISSION HOS C. A. REITZEL
BIANCO LUNOS BOGTRYKKERI
1909

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REMARKS ON THE METAMORPHOSIS AND DISTRIBUTION OF THE LARVAE OF THE EEL (*ANGUILLA VULGARIS*, TURT.)

BY

JOHS. SCHMIDT

WITH ONE PLATE AND ONE CHART

KØBENHAVN
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I. Introduction.

THE following paper is issued as a supplement to my previous work: "Contributions to the life-history of the Eel (*Anguilla vulgaris*, Turt.)" published in 1906 in "Rapport de la Commission C. 2, Vol. V des Rapports et Procès-Verbaux du Conseil International pour l'Exploration de la Mer", Copenhague 1906. It contains some information and experiences gained on cruises with the "Thor" after the work mentioned had been published, besides some new investigations on the metamorphosis of the eel, made by means of a far better and more comprehensive material than was at my disposal when I wrote the first paper.

As one of the chief objects of the cruise of the "Thor" in the Atlantic in 1906 was to extend the investigations from 1905 on the larvae of the ordinary fresh-water eel, much new material was of course obtained during this cruise. A list of the larvae caught was already published in the paper in 1906 (p. 249—255) but otherwise there was then no time left for entering into details of the results. In 1907 the "Thor" was not out in the Atlantic but confined her investigations to the Skager Rak and the Danish waters. On the other hand in 1908 on our way to Iceland we investigated a line from the Hebrides out to Rockall, and during this voyage we again caught eel larvae, the places of occurrence of which are in an interesting way supplementary to our former investigations.

We have now taken altogether ca. 800 specimens of the eel in the larval stage, a great number of which (from September 1906) are in process of metamorphosis, while the former material of metamorphosing stages (see the 1906 paper) in fact only consisted of a few specimens (8).

The material from 1908 originates from two different periods, namely (1) from May and June and (2) from the first half of September and the last days of August. While all the upwards of 200 specimens from May and June 1906 like all the ca. 265 specimens from June 1905 were in the 1st Stage a and b (see l. c., p. 249), and consequently had not yet begun the retrogressive metamorphosis, the latter was the case with the majority of the specimens from Sept. 1906 (upwards of 300 in all)[1]. Thus, the row of teeth was only intact in ca. 11 % of these, but even among these 11 % we found none in which the digestive tract was still very thick and strong, which was most often the case with our specimens from the early summer. The circumstance that none of the specimens from the early summer were in process of metamorphosis, while this was the case with the majority of the specimens from September, is a very important fact which confirms the view[2] formerly expressed by me that the propagation of the eel does not take place all the year round (at any rate not on the same scale throughout the year) as might perhaps have been expected for a deep-water fish, but that the propagation in the main is limited to certain times of the year.

[1] As will be seen from the list (l. c., p. 252—255) the majority of the specimens were in Stages 2 and 3, but otherwise all Stages from I b to IV b were represented.

[2] In the 1905 investigations I had only 8 specimens from September for my guidance, hence the upwards of 300 specimens to hand from the autumn of 1906 show a considerable increase of material.

The material from 1908 was obtained at the end of the month of May and only contains specimens in the 1st Stage, but as already mentioned it is of interest as it widens our knowledge of the distribution of the larvae.

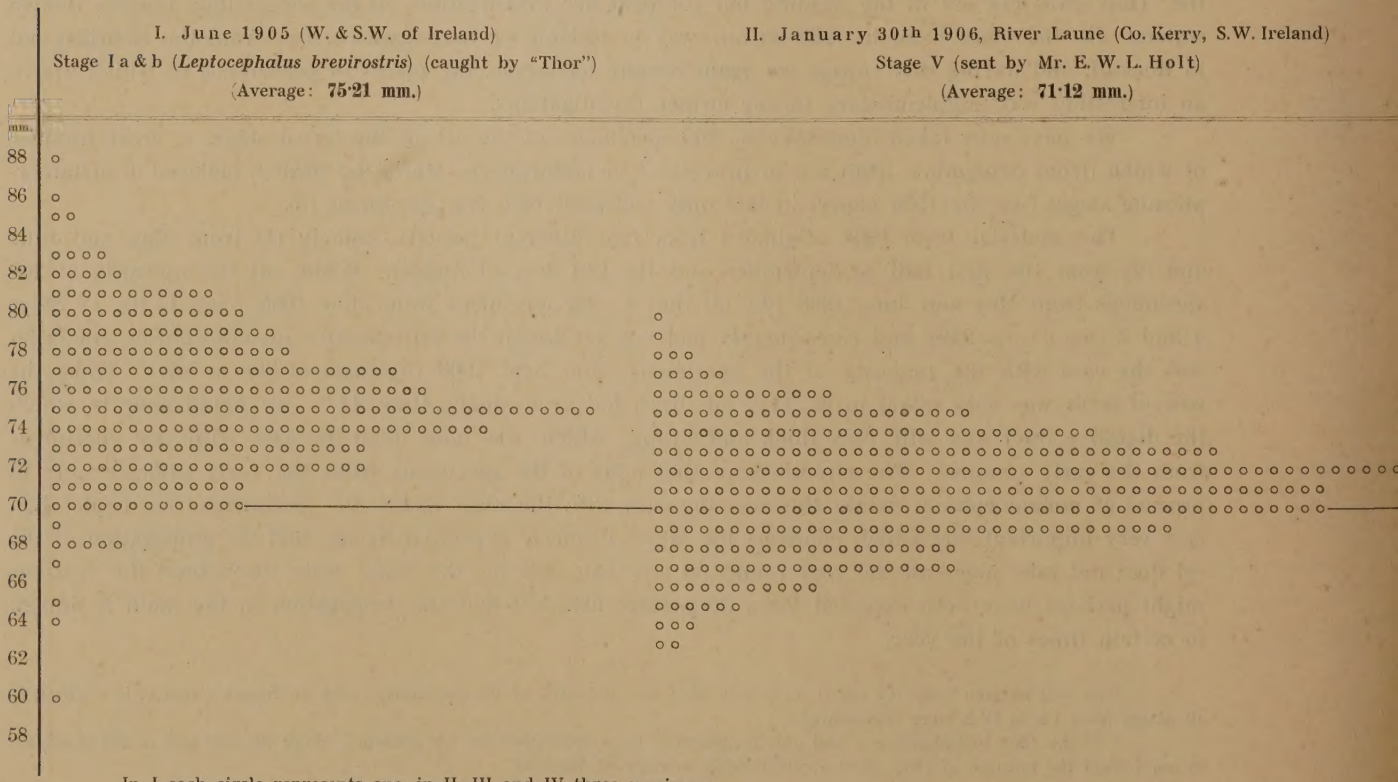
As seen from the above, the later investigations confirm in the main the results obtained in 1905. There are however some points which need to be corrected, and this has been made possible by means of the better material now to hand.

In the following pages we shall principally deal with (1) the history of the metamorphosis of the larval eels and (2) their distribution in the Atlantic.

II. Metamorphosis of the larvae of the eel.

Though the Leptocephali to begin with keep well in the preservative solution most frequently used, namely weak formaline, they generally after some time begin to swell, until at last they get perfectly bag-shaped, quite unlike the living animals. Directly after the return of the "Thor" in September 1906, part of the material of *Leptocephalus brevirostris* as well as of other species of Leptocephali was therefore photographed in order to get the best pictures possible of these animals, which then, only a

Tab. I. Graphic representation of the reduction in the to



In I each circle represents one, in II, III and IV three specimens.

few weeks after the capture, had still practically the same appearance as the living animals. A selection of these photographs representing the different stages of the metamorphosis is reproduced on Pl. I; the photographs are magnified direct from nature (ca. $2^1/_2$ nat. size), and they illustrate much better than my former figures how the larvae during metamorphosis keep their glass-clear appearance, which makes all the segmentation in myomeres distinctly seen. The exterior of the eyes is also more correctly figured, as it is seen that the iris is light (silver-coloured), while on the former figures it was black. (These figures were reproductions from photographs of specimens preserved for a longer time, when the eyes gradually become quite black).

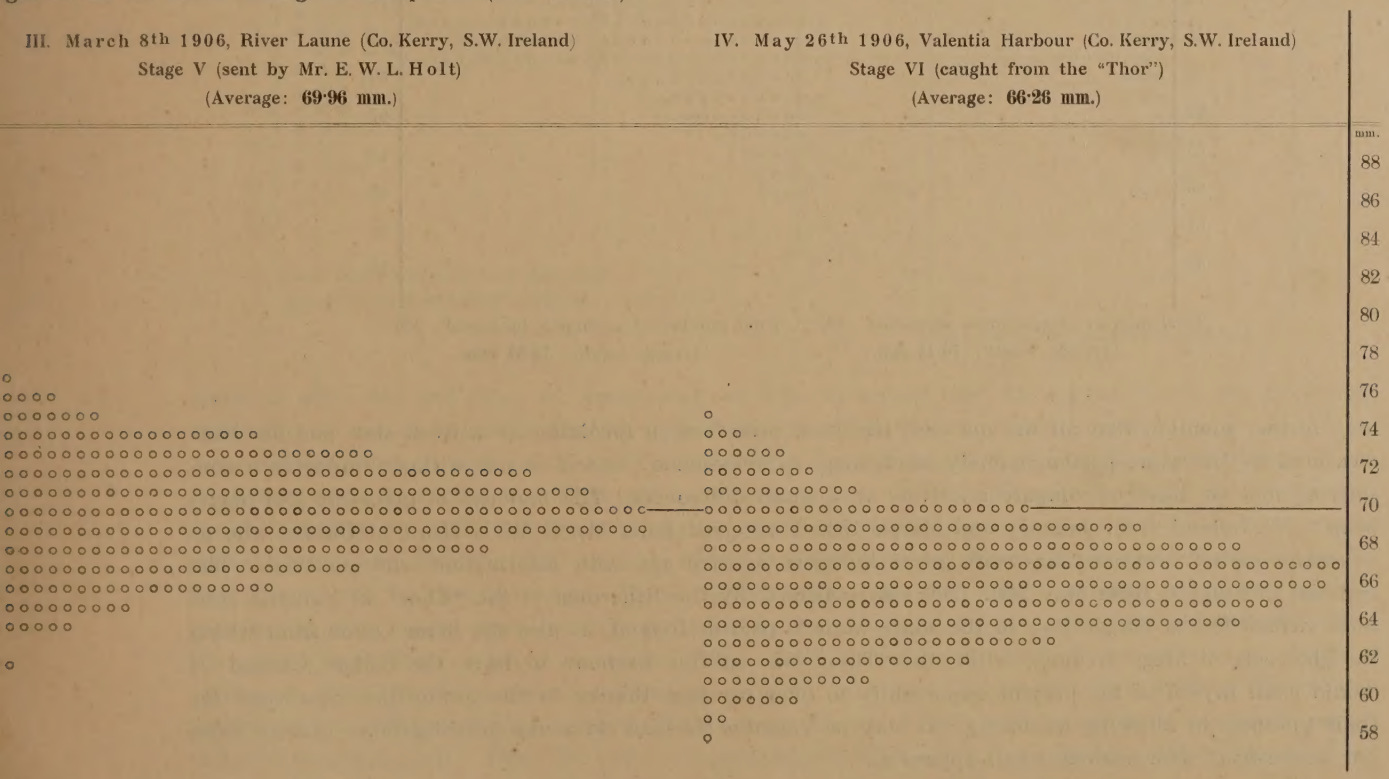
In contrast to the former figures those reproduced here also more correctly show the reduction in length during the metamorphosis, because the separate stages have been photographed at the very size which corresponded to the standard size of a certain stage. For the present Pl. I I have as far as possible chosen such specimens as were in a different stage of the metamorphosis than those previously figured by me.

I may begin with discussing the reduction in length during the metamorphosis, afterwards setting down some remarks on the reduction in weight which takes place at the same time.

A. Reduction in length during the metamorphosis.

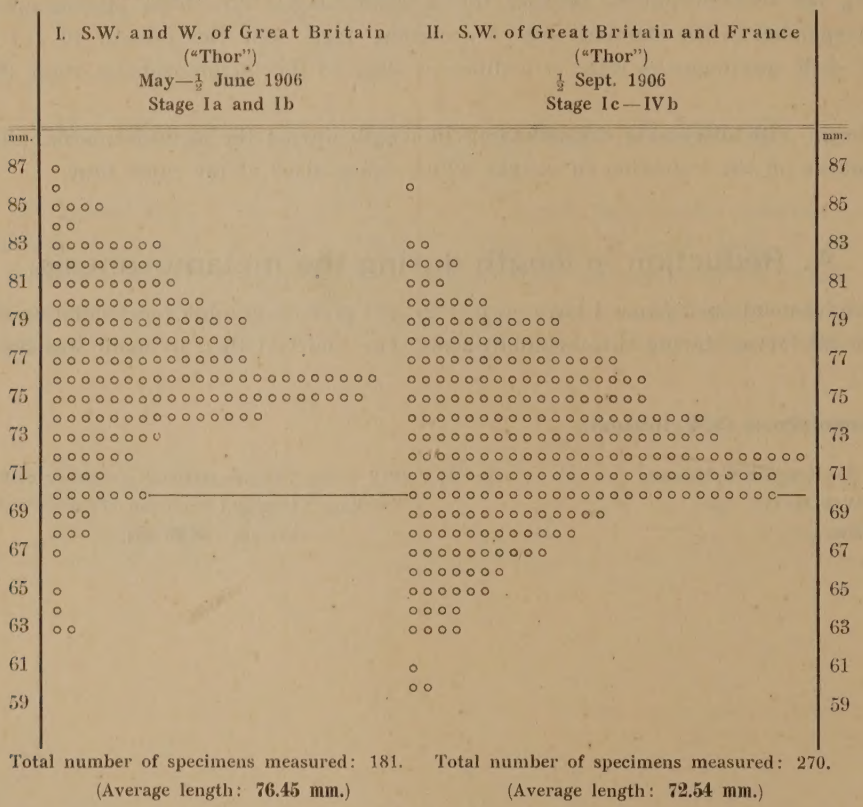
In the above-mentioned paper I have on p. 172—173 given a graphic representation of the reduction in length of the eel larvae during the metamorphosis. The material then to hand was far from being so

ngth of the eel larvae during metamorphosis (S.W. Ireland)



complete and uniform as that now in my possession. At that time I was obliged to compare Leptocephali (1st Stage) from June 1905 with glass-eels (5th Stage) from March and April 1905 and with the 6th Stage from June 1899, etc. i. e. specimens from quite different year-groups. — On the other hand the material now before us is as uniform as possible; it consists of (1) Leptocephali (1st Stage) from June 1905 taken S. W. of Ireland by the "Thor" and (2) glass-eels (5th and 6th Stage) taken the following winter and spring in the south-western part of Ireland. We are thus able to compare Leptocephali and eel fry both of which originate from the same place and belong to the same year's group. I

Tab. II. Atlantic Ocean W. of Great Britain and France.



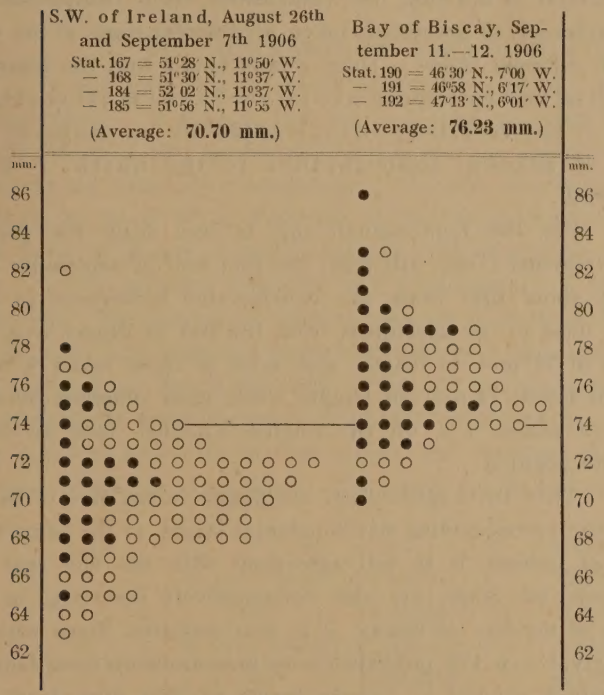
Total number of specimens measured: 181. (Average length: **76.45 mm.**)

Total number of specimens measured: 270. (Average length: **72.54 mm.**)

may further mention that all the material has been preserved in formaline in a fresh state and has been measured by the same person, namely cand. mag. A. Strubbebg, which is not without importance considering that we have to compare relatively very small differences. The material of glass-eels (5th Stage) from S. W. Ireland from January and March 1906 I received from Mr. E. W. L. Holt of Dublin who as on many earlier occasions has with great kindness assisted me with information and material. The material of Stage 6 from May 26th 1906 was collected by the fishermen of the "Thor" in Valentia Harbour (which lies at Dingle Bay in the south-western part of Ireland, as also the River Laune from which the glass-eels of Stage 5 came), while the "Thor" was in this harbour to have the boilers cleaned. I would avail myself of the present opportunity to offer my best thanks to the authorities concerned for their kindness in allowing us during our stay in Valentia Harbour to make investigations inshore from our motor-boat with various small apparatus.

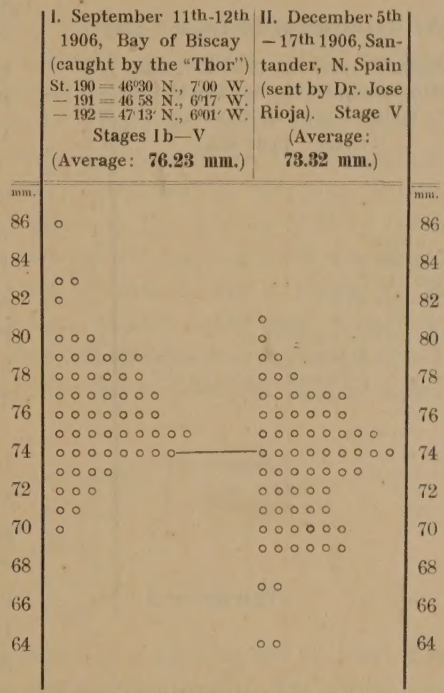
In the accompanying Table I is shown the result of the measurements. While the Leptocephali at Stage 1 in June 1905 had an average length of *75·21* mm., we see that the glass-eels of the same year in Stage 5, caught in S. W. Ireland on the last days of January 1906, had an average length of 71·12 mm. From June till the end of January they have thus on an average decreased ca. 4 mm. in length. In March the average length of the glass-eels in Stage 5 was 69·96 mm. and lastly at the end of May the average length of Stage 6 was 66·26 mm. From June 1905 till the end of May 1906 the reduction in the length was thus ca. 1 cm. on an average, and as no further reduction of any importance seems to be

Tab. III. Leptocephalus Anguillæ vulgaris
St. Ib—IVb (caught by the "Thor").



Each circle represents one specimen.
● represents a specimen belonging to stage II.

Tab. IV. Graphic representation of the reduction in the total length of the eel larvae during metamorphosis (Bay of Biscay)



Each circle represents one specimen.

going on after May and June, we are scarcely in error in saying that the eel larvae are on an average reduced ca. 1 cm. in length during the metamorphosis which lasts up to ca. 1 year.

From Table II page 6 we see that in 1906 the average length of the Leptocephali in Stage 1 was 76·45 mm. while in 1905 it was 75·21 mm. (see Table I, p. 4—5) this difference in length is possibly due to the fact that the 1906 material of Stage 1, consisting of full-grown larvae, was taken ½—1 month earlier in the year than the 1905 material which thus perhaps had already begun the reduction in length. But it may also be that the length of the larvae varies from one year to another. That this actually may be the case is seen from a study of the Tables I p. 4—5 and III p. 7. We thus see that in Table I the glass-eels of Stage 5 taken on January 30th 1906 in south-west Ireland had an average length of 71·12 mm. while the Leptocephali of Stage 2—4 taken in August—September 1906 S. W. of Ireland (belonging to the next year's group) only had an average length of 70·70 mm. though they were in an earlier stage of metamorphosis. Thus, the case is more complicated than was supposed at first sight, and we

are therefore not justified in comparing the developmental stages of different year-groups as I did in my first paper, for want of sufficient material. In comparing measurements of migrating glass-eels we must be prepared to find that the reduction, under the influence of quite local outer conditions (salinity etc.), does not take place equally rapidly even at places which lie near each other (cf. the measurements of glass-eels from San Sebastian Table V with those from Santander Table IV which were taken not much earlier). It is for example not unlikely that the influx of the animals into pure freshwater hastens the reduction, the correctness of which supposition however has not been proved, and it may also be that there are small differences in size already in the leptocephalic stage.

In another respect also later investigations show that if we want to find the extent of the reduction in length of the eel larvae we must be very careful in drawing our conclusions from comparisons of measurements of specimens taken at different times of the year and at different places. Thus, it was found that the glass-eels as well as the Leptocephali are larger in the most southern part of the territory investigated by us, namely the Bay of Biscay, than further to the north, e. g. at Ireland.

Tab. V. Transparent Elvers (5th Stage)

mm.	December 1906, Ria Orio, San Sebastián (Spain), sent by the Danish Vice Consul Jorge J. Mueller. (Average: **75.64 mm.**)	Number of Specimens
84	o	1
	o o o	3
82	o o o o o o	6
	o o o o o o o	7
80	o o o o o o o o o	9
	o o o o o o o o o	9
78	o o o o o o o o o o o o o o o o o	17
	o o o o o o o o o o o o o o o	15
76	o o o o o o o o o o o o o o o o o o o o o o o	23
	o o o o o o o o o o o o o o o o o o o o	21
74	o o o o o o o o o o o o o o	14
	o o o o o	5
72	o o o o o o o o	8
	o o o o o o	6
70	o o o o o o o	7
	o o o	3
68	o o o o	4
	o o o	3
66		
	o o	2
64	Total specimens . .	163

For the Leptocephali this is seen from the present measurements (Table III) from the first half of September 1906 which show that there are considerable differences in size. Thus, most of the specimens from the Bay of Biscay were upwards of 74 mm. in length, and most of those taken S. W. of Ireland below 74 mm. in length, while those obtained between the two places, i. e. off the English Channel, held an intermediate position.

That the Leptocephali are larger in the Bay of Biscay than the corresponding developmental stages at the same time S. W. of Ireland, is in full agreement with the fact that the glass-eels (5th Stage) are also comparatively very large on the coasts of the Bay of Biscay, e. g. near Bayonne, from which I formerly (l. c., p. 172) published some measurements from January 1906 which showed an average length of 73·51 mm. I got this point further confirmed on measuring glass-eels from the Spanish north coast (San Sebastian, Bilbao and Santander). I give here the measurements from Santander (Table IV), at the same time stating that I am indebted to the Director of the Marine Biological Station there, Dr. Jose Rioja, for the well-preserved, formaline material. The measurements show at once that the glass-eels were very large, and on calculating the average size this is found to be 73·33 mm. which is almost the same as that of the Bayonne specimens from the beginning of January 1906; the measurements from San Sebastian (Table V) and Bilbao show the same or a still greater length. We may therefore now consider it as an established fact that besides the Leptocephali also the glass-eels (5th Stage) are on an average larger in the Bay of Biscay than further to the north in the territory investigated by us. But we see from this that it was not justifiable to compare glass-eels from Bayonne with Leptocephali taken W. and S. W. of the British Isles as I did formerly (l. c., p. 172) in order to gain information on the reduction in length that takes place during the metamorphosis.[1] On the contrary we must, as above, compare glass-

[1] We may conclude here that the remarks made by me (l. c., p. 172, note 1) are incorrect. At that time I took it for granted that the rule which applies to so many other of our food-fishes, namely, that the pelagic fry of the same species are larger (at the same developmental stages) in the northern waters than further to the south, would also apply to the eel. This is however not the case as regards the eel nor as regards various other species, which proves that there are several exceptions from this rule.

eels from Great Britain (Ireland) with Leptocephali from the waters off Great Britain and again glass-eels from the coasts of Biscay with Leptocephali from the Bay of Biscay. In spite of the error thus committed in my previous work by using specimens from the Bay of Biscay (Bayonne) for my calculations of the reduction in length during the metamorphosis, the final result is approximately correct so far as the total reduction in length from Stage 1—6 is concerned, the reason being that both the extremes measured at the time, namely Stages 1 and 6, comprised specimens from the northern part of the territory (from W. of the British Isles and from the North Sea respectively). Thus, the measurements published here in Table I, and better and more uniform in respect to time and place can hardly be procured, confirm the main result: that the eel-larvae during metamorphosis are reduced ca. 1 cm. in length.

B. Reduction in weight during the metamorphosis.

In the preceding we have only dealt with the reduction in length that takes place during the metamorphosis. It appears that this reduction in length (and in height) is attended with a reduction in weight, which is only natural considering that the animals for several months, perhaps varying according to place, do not take any nourishment. The two following series of weighings, which were most kindly made (I) by Dr. F. Weis, Professor at the Royal Danish Veterinary and Agricultural College and (II) by cand. polyt. H. Jessen-Hansen, assistant at the Carlsberg Laboratory, illustrate this reduction in weight.

I. The material consisted of 7 Leptocephali in Stage 1 taken in the Atlantic S. W. of Ireland in June 1905. The specimens were so selected that all of them had the average length of this stage, i. e. ca. 75 mm. The material comprised besides 7 glass-eels in Stage 5 taken in the R. Laune (Co. Kerry, S. W. Ireland) on March 8th 1906. They all had the average length, namely ca. 70 mm. According to a communication from Professor Weis the "fresh-weight" was determined after the superficial liquid had been removed by means of filter paper, and the "dry-weight" after the preparations had been dried in an oven at 100° for 1—2 days. The result was as follows:

	"Fresh-weight"	"Dry-weight"	"Dry-weight" in % of "Fresh weight"
1) 1st Stage (7 spec.).....	10·353 gr.	0·756 gr.	*7·30 %*
do. (Average).....	*1·479* -	*0·108* -	
2) 5th Stage (7 spec.).....	2·293 -	0·465 -	*20·12 %*
do. (Average).....	*0·328* -	*0·066* -	

II. The material for the other series of weighings consisted of 5 Leptocephali in Stage 1 of the average length and of 32 glass-eels in Stage 5 which also had the average length. The Leptocephali as well as the glass-eels originated from the same samples from which the specimens mentioned under I had been selected. According to a communication from cand. polyt. H. Jessen-Hansen the "fresh-weight" was determined by weighing the animals after carefully drying in filter paper and the "dry-weight" by drying to constant weight in a vacuum at ca. 85° C. The result was as follows:

	"Fresh-weight"	"Dry-weight"	"Dry-weight" in % of "Fresh-weight"
1) 1st Stage (5 spec.).....	7·006 gr.	0·1908 gr.	*5·57 %*
do. (Average).....	*1·401* -	*0·0782* -	
2) 5th Stage (12 spec.).....	4·071 -	0·8277 -	*20·3 %*
do. (Average).....	*0·339* -	*0·069* -	
3) 5th Stage (20 spec.).....	6·150 -	1·2334 -	*20·2 %*
do. (Average).....	*0·308* -	*0·0617* -	
Average of all the 32 spec. of Stage 5.....	*0·319* -	*0·0644* -	*20·2 %*

These determinations show, just as we were really justified in expecting, that the Leptocephali as well as the glass-eels vary individually a good deal in weight but, on the other hand, there is complete agreement that there is a considerable loss of weight, both in the "fresh-weight" and the "dry-weight", during the metamorphosis from Stage 1 to Stage 5. This is illustrated by the following summary of the average numbers obtained by the investigations I and II:

	Investigation I.		Investigation II.	
One specimen (average):	1st Stage (7 spec.)	5th Stage (7 spec.)	1st Stage (5 spec.)	(5th Stage (32 spec.)
"Fresh-weight"	1·479 gr.	0·328 gr.	1·401 gr.	0·319 gr.
"Dry-weight"	0·108 -	0·066 -	0·0782 -	0·0644 -
Dry-weight in % of fresh-weight	7·30 %	20·12 %	5·57 %	20·2 %

and by having the average loss of weight calculated on the basis of all the specimens investigated (12 spec. of 1st and 39 of 5th Stage):

Average loss of weight during the metamorphosis from the 1st to 5th Stage:

Loss of	Gram	in % of average weight of 1st Stage
"Fresh-weight"	1·126	77·82 %
"Dry-weight"	0·031	32·29 %

Referring for the rest to the above numbers I need only here point out some special conditions. On an average 691 specimens of Leptocephali of Stage 1 and 3112 glass-eels of Stage 5 represent 1 kilogram in weight[1]. We thus find that the Leptocephali in the fresh state weigh on an average between 4 and 5 times more than the glass-eels. During the metamorphosis from Leptocephalus of the 1st Stage to the glass-eel of the 5th Stage the animals thus become greatly reduced in weight, namely no less than 77·82 % of the original weight on an average. It is not the very great loss of water alone which makes the loss of weight so strikingly great, for if we calculate how much the animals are reduced in dry-weight we find that this loss is also very considerable, namely 32·29 % on an average or no less than a third of the original dry-weight. We have here for the first time obtained a definite proof of the fact that a consumption of the substance of the body is actually going on during the metamorphosis, which for the rest might have been foreseen considering that the metamorphosis coincides with a long fasting-period during which the animals take no nourishment[2].

I may for the rest point out that the above numbers do not even represent the loss of weight during the whole metamorphosis, i. e. right from the 1st to the 6th Stage, but only the loss of weight from the 1st to the 5th Stage. The reason why I did not try by weighings of the entirely metamorphosed dark-coloured "Montée" of the 6th Stage to determine the loss of weight during the whole metamorphosis is, that the fry take food during the transition from the 5th to the 6th Stage, which thus makes the matter still more complicated. All the glass-eels weighed were therefore colourless specimens about which I had ascertained that their digestive tract did not contain any food whatever[3].

[1] This corresponds very well to the statements of the weight of the glass-eels reported by the English fishermen on the Bristol Channel, according to which "1400—1500 elvers make one lb" (see my paper from 1906, p. 201).

[2] Besides the above determinations of the loss of weight during the metamorphosis Professor Weis and cand. polyt. Jessen-Hansen have made some determinations of the nitrogen and fat contained in the Leptocephali and the glass-eels respectively, but it has been found that a greater material than was at present available would be necessary in order to obtain trustworthy results as to the kinds of stuffs which are principally consumed during the metamorphosis. When a larger material is available we may return to this question.

[3] I take this opportunity to remark that, in my former paper I have been guilty of an inaccuracy in putting the case (p. 175) as if the eel-fry never take any nourishment until the whole metamorphosis is completed and the animals have entered into the black 6th Stage. In reality I have afterwards occasionally found that the intestinal tract of very faintly pigmented glass-eels of Stage 5 B. taken in the sea contained copepods, and according to kind information from Dr. A. Bowman in Scotland he has

Moreover I may call attention to the fact that the investigation on the weights exclusively refers to specimens belonging to the smaller, more northerly "stock" from the waters of the British Isles. If we had weighed Leptocephali and glass-eels from the Bay of Biscay we should have obtained other and larger numbers.

C. Change of colour during the metamorphosis.

In his recently pnblished work on the eel (Annal. Soc. Roy. Zool. Malacol. de Belgique, XLIII, 1908) GILSON has thoroughly discussed the question of the pigmentation of the glass-eels during the metamorphosis from the 5th to the 6th Stage; hence I cannot add anything new of importance. I may however here set forth some few remarks respecting the conditions for the commencement of the pigmentation. Owing to VAILLANT's statement to the effect, that the metamorphosis proceeds specially rapidly when the animals have come into fresh water (see my paper of 1906, p. 198, where VAILLANT's statements are cited), I made in 1906 on board the "Thor" some experiments by placing colourless glass-eels respectively in fresh and salt water (from the North Sea). In all cases the animals became pigmented in the course of a shorter or longer time, though somewhat more rapidly in the fresh than in the salt water, but the difference was not so great that it could be considered as having been proved to a certainty, because some of the specimens placed into salt water became even more rapidly pigmented than some of those in the fresh water, so that we could not know for certain how great was the influence exercised by individual differences compared with the possibly accelerating influence of the fresh water on the metamorphosis. But from these experiments it is at any rate evident that the commencement of the pigmentation is principally due to a quality inherent in the animals, which is in operation whether the animals live in fresh or in salt water. I had later an opportunity to observe a crucial instance of this during the "Thor's" stay in the Atlantic S. W. of Ireland. On the 22th of May 1906 a pelagic glass-eel in Stage 1 A was caught near the surface of the water at station 56 (51° 24′ N., 10° 20′ W.) This specimen which was entirely lacking in pigment except at the tail was placed in an aquarium together with a number of Leptocephali in Stage 1 in pure oceanic water of a salinity of 35·30—35·40 ‰, i. e. extremely salt water, such as is only found out in the Atlantic proper. This glass-eel was now kept together with the Leptocephali for a couple of weeks under the above-described conditions. It became rapidly pigmented, so that already in the middle of June it was almost quite black.

We thus see that the glass-eels become pigmented whether they live in salt or in fresh water, and most likely the other part of the metamorphosis also proceeds independently of this. It would for the rest be a very interesting task for those who have facilities for making aquarium experiments on a larger scale and under more favourable conditions than the very primitive ones offered by a rolling ship, to investigate to what extent the rapidity with which the metamorphosis proceeds is influenced by outer factors.

made the same experience. Moreover, among some eel young with incipient black pigmentation, which I kept in an aquarium with salt water on board the "Thor", I have seen some greedily pursue the copepods which were placed together with them. It was however especially the darkest specimens, i. e. those approaching Stage 6 which did so, whereas the younger, colourless specimens generally appeared quite indifferent to the nourishment put into the water near them. Though in fact, it has been found that the rule is not without exceptions, this cannot alter the main point, namely, that the colourless glass-eels generally do not take any nourishment, This is for the rest no peculiarity considering that we are dealing with animals in process of metamorphosis, during which it is the rule that no nourishment is consumed.

III. Distribution of the larvae of the eel.

A. 1st—4th Stage.

From the Chart Pl. II, on which all the stations where we used the young-fish trawl in 1903, 1904, 1905, 1906 and 1908 have been marked, as far as space permitted it, it will be seen at which of them the eel larvae of the first 4 stages occurred and at which they were absent.

The Chart shows that the larvae were found over the whole of the long stretch from W. of the Færoes to the north coast of Spain. The most northerly place of discovery W. of the Færoes must be considered as approximately marking the northerly limit for the distribution of the larvae in the eastern part of the Atlantic, for we have already made so many hauls north of this place round Iceland that it is certainly quite out of the question that the eel larvae could have escaped us altogether here if they had occurred in quantities (see the Chart Pl. X in my paper of 1906). But while the northern limit for the distribution and therefore also for the spawning-ground of the eel may be said already to be determined with some correctness, it is not to be thought that our most southerly places of discovery near the Spanish north coast mark the southern limit for their distribution. On the contrary, we must certainly take it for granted that the eel propagates and that eel larvae are found further to the south off the coast of Portugal and the north-western part of Africa, as far as the temperatures and the salinity in deep water will allow, and that the only reason why they have not yet been found there is that no suitable investigations in the Atlantic south of the Bay of Biscay have as yet been made.

It will be seen that on the Chart we have made a distinction between the Leptocephali of the 1st and of the 2nd—4th Stage; moreover, the stations in early summer (May-June) and in late summer (August-September) have been discriminated by different signs. We thus observe at once that all the specimens from the early summer, whether they were taken off the most northerly part of Scotland or in the most southerly part of the Bay of Biscay, were in Stage 1, while on the other hand by far the greater number of those taken in August-September had already passed Stage 1.

From the Chart it appears that the eel larvae in the Atlantic W. of the English Channel occur far out to sea, at least as far to the west as ca. 15° W. L. If we examine at what places the youngest developmental stage we know (1st Stage) has been taken, we find that it occurs, e. g. S. W. of Ireland, everywhere outside a depth of ca. 1000 m. but irrespective of how great the depth otherwise may be, thus at the greatest depths where the "Thor" has been, namely ca. 5000 m.[1] This is a peculiar and very unusual circumstance, which according to my opinion may perhaps be explained thus that the propagation of the eel takes place bathypelagically out in the ocean far from the coasts but irrespective of the bottom. It would however be superfluous to discuss this question so long as we know no more than we do now.

Further, the Chart distinctly shows that the youngest developmental stages (1st Stage) are generally found far out to sea, farther from the coastal plateau than the later developmental stages (2nd—4th) which, in fact, we found in quantities in August and September 1906. For further illustration of this fact I may give the catches at 3 series of stations which lie S. W. of Ireland, off the English Channel and in the Bay of Biscay, the stations within each of the 3 series having been chosen so that the first lies as far as possible outside, the second close by, and the third inside the 1000 m. curve. All the stations were investigated by the "Thor" during the first part of September (and the last days of August) 1906,

[1] It is worth noticing that during the investigations made in September 1906 at great depths W. of the English Channel, the comparatively few specimens of the eel larvae which still were in the 1st Stage were principally found at the greatest depths furthest from the coastal plateau with depths less than 200 m., while the specimens taken nearer the plateau generally were in a far more advanced stage of metamorphosis, for I am of opinion that this indicates the fry to have mainly come from out here even though other quantities may have been produced nearer the coastal plateau.

i. e. at a time when the majority of the specimens were in process of metamorphosis, while some of them, however, had not yet passed the 1st Stage.

Series I. Bay of Biscay.

1) St. 190. 46° 30′ N., 7° 00′ W., Depth: > 4000 m.:
Stage I b: 8 specimens.
— I c: 13 —
— II: 23 —

2) St. 191. 46° 58′ N., 6° 17′ W., Depth: > 3000 m.:
Stage I c: 1 —
— II: 12 —
— III: 1 —

3) St. 193. 47° 13′ N., 6° 01′ W., Depth: 950—210 m.:
Stage II: 2 —
— III: 1 —
— IV a: 1 —

Series II. Off the English Channel.

1) St. 180. 48° 19′ N., 13° 53′ W., Depth: > 4000 m.:
Stage
— I b: 3 —
—

2) St. 181. 49° 22′ N., 12° 52′ W., Depth: 1350 m.:
Stage I b: 1 —
— II: 1 —

3) St. 186. 50° 06′ N., 11° 06′ W., Depth: 600—470 m.:
Stage I b: 6 —
— I c: 8 —
— II: 56 —
— III: 30 —
— IV a: 10 —
— IV b: 2 —

Series III. S. W. of Ireland.

1) St. 167. 51° 28′ N., 11° 50′ W., Depth: 1350—1160 m.:
Stage I b: 3 —
— II: 3 —
—

2) St. 168. 51° 30′ N., 11° 37′ W., Depth: 390 m.:
Stage I b: 5 —
— I c: 1 —
— II: 20 —
— III: 21 —

Once more pointing out that in May and June all the specimens were in Stage 1 a and b, whether they occurred near or far from the 1000 m. curve, the above summary offers an excellent view of the occurrence of the various metamorphosing stages. Thus it is seen that in each of the 3 series there is a distinct difference between the stations as to the developmental stage of the eel larvae which were taken there. At the stations of all 3 series which lie nearest to the coasts (St. 193, 186 and 168) most of the larvae were in an advanced stage of the metamorphosis, at the most distant stations there was a much greater percentage of specimens in Stage 1, while at the intermediate stations they held in this respect an intermediate position.

We thus see (cf. also the Chart Pl. II and the detailed list given in my paper of 1906, pp. 252—255) that there is a distinct difference in the distribution of the various developmental stages, according as the locality is near or far from the coastal plateau. Thus, while only comparatively few specimens of Stage 1 were found inside this place (1000 m. curve) great numbers of the later stages (2nd—4th) were on the other hand taken here, which shows that the larvae during the metamorphosis from the 1st to

the 4th Stage migrate inshore towards the coasts from the greater depths. As will be seen from the Chart Pl. II this migration seems however to proceed rather slowly, at any rate as regards the part of the territory which lies S. of Ireland, but it has however in some cases been known to proceed at a greater speed. This is indicated, as marked on the Chart, by the Scotch investigation-steamer "Goldseeker's" discovery of a Leptocephalus in Stage 1 north of Scotland in July ("Sc.") and still more by the fact that according to kind information from Dr. HELLAND-HANSEN of Bergen, he found in October 1907 an eel larva in the 3rd Stage amongst the fringe of islands near Bergen ("N.").

From our investigations in 1904—08 the fact has been established that the larvae of the eel are of constant occurrence in the sea W. of the British Isles and France outside the coastal plateau and are to be caught there by means of suitable apparatus in as great numbers as the pelagic fry of other important useful fishes may be caught elsewhere. Out here they occur year after year in striking quantities considering how great are the areas in horizontal as well as in vertical direction over which they are spread, in fact, there are places where the larva of the eel is the most commonly occurring pelagic fish. To exemplify this I may mention our Station 190 on the 11th of September 1906 in the Bay of Biscay at 46° 30′ N. and 7° 00′ W. over a depth between 4- and 5000 m. In a 2 hour's haul with the young-fish trawl at a depth of ca. 30 m. below the surface we obtained, besides several (ca. 30) liters of the pteropod *Cymbulia*, the following fish young: 1 Arnoglossus, 37 Scopelini, 5 specimens of fry of an unknown fish, 30 specimens of pelagic needle-fishes, and finally 43 larvae of the ordinary eel, which thus outnumbered all the other species of fish occurring there. We thus see that there are places where the larvae of the eel are the commonest fish, just the same as is the case with those of the cod, the herring etc. at other places.

From the above haul it is seen that the larvae occurred in quantities as high up in the water as ca. 30 m. below the surface, and I may add that we have had the same experience several other times and that after all we have till now never taken them in larger numbers than near the surface (at St. 186 8th Sept. 1906, 50° 06′ N., 11° 06′ W. in a haul at a depth of ca. 30 m. we thus took the greatest number hitherto obtained viz. 55 per ½ hour), but it was however only during the night that they appeared in quantities so high up in the water. St. 185, 7th Septb. 1906 (51° 56′ N., 11° 55′ W.), provides fairly good information on their vertical movements in the course of a day and night, as can be seen from the following hauls:

1)	young-fish	trawl	300	m.	wire,	from	8·35	to 9·35 a. m.	....	0	larvae
2)	—	—	600	-	—	—	10·00	- 11·00 —	....	1	—
3)	—	—	900	-	—	—	11·35 a. m.	- 12·35 p. m.	....	8	—
4)	—	—	900	-	—	—	1·45 p. m.	- 2·45 —	....	10	—
5)	—	—	900	-	—	—	4·10 —	- 6·10 —	....	0	—
6)	—	—	600	-	—	—	6·45 —	- 7·45 —	....	1	—
7)	—	—	300	-	—	—	8·30 —	- 10·30 —	....	18	—
8)	—	—	250	-	—	—	11·00 —	- 12·00 —	....	4	—

Daylight. Darkness.

From haul 1 and haul 7 we see the difference between day and night: haul 1 which was made in broad daylight gave no larvae, while on the other hand haul 7, made at the same depth (ca. 150 m. below the surface) but in darkness, gave no less than 18 specimens. I explain it thus, that by day the Leptocephali stay further down in the water than by night, like so many other pelagic animals. We therefore see that both the hauls 3 and 4, made in broad daylight but at a great depth (ca. 4—500 m. below the surface) gave larvae. On the other hand the hauls 2, 5 and 6 must be considered as transition-hauls made at the times during a day and night, when the larvae were moving downwards and upwards respectively, and when only 4 larvae were taken in haul 8, which was made highest up in the water of all the hauls

at this station, this may undoubtedly be explained in this way that they were now, i. e. in the middle of the night, still nearer the surface than the net which was dragged at a depth of ca. 125 m., for by numerous other hauls at other stations I have proved with certainty that the majority of the larvae in the dark nights late in the summer are in movement higher up in the water, at a depth of ca. 25 m. below the surface or thereabout.[1]

The investigations made out in the Atlantic in winter are of course not by far so comprehensive as in summer, and the "Thor" has till now never been out on a winter cruise here. The Irish investigation-steamer "Helga" has however on its quarterly cruises occasionally caught larvae or metamorphosing stages of the eel also during the winter months, namely in November and February, and through the kindness of Mr. E. W. L. Holt, the Director of the Irish investigations, I have had the opportunity to investigate several of them (see my paper of 1906, pp. 196, 216, 217). Apart from a single exception all the specimens from the winter-months were in an advanced stage of metamorphosis, which is in full agreement with the fact that all the several hundreds of specimens from the early summer were in the 1st Stage, and that the migration of the glass-eels is limited to certain months of the following winter and spring differing according to the position of the place.

The only exception from this theory known as yet is a specimen in the 1st Stage B., which was taken on February 5th 1906 W. of Ireland by the Irish investigation-steamer "Helga" (Stat. S. R. 302, 51° 54′ N., 11° 54′ W., Depth: 460 fms.) at a depth of 200—350 fms. below the surface. The specimen is 73 mm. long, its row of teeth is intact, but the digestive tract already somewhat reduced in thickness shows that it belongs to my 1st Stage B., hence it is likely that we have to deal with a laggard of the year's group, the greater number of which at this time of the year already approach the end of the metamorphosis, namely the glass-eel stage (5th Stage). If so, I think we may place this discovery along with the formerly mentioned discovery (p. 11) of a pelagic glass-eel S. W. of Ireland on May 22th 1906, i. e. at a time of the year when otherwise we only found larvae of the 1st Stage belonging to the next year here. For the present these isolated discoveries must be considered as exceptions from the rule: that Stage 1 occurs in spring and summer, especially in the early summer, the later developmental stages (2nd—4th) in the later summer, the autumn and the beginning of the winter, while the glass-eel period is in winter and spring.

B. 5th Stage.

The publication in 1906 of my first paper on the eel has in different quarters led to investigations on the migration of the eel and the time for its ascent into fresh-water, so that there is now every prospect of gradually getting this question thoroughly discussed, since the interest for it has increased so considerably. There is here every reason to mention the experiments made by Gilson (l. c., pp. 40—45) for the purpose of determining when the glass-eels arrive from the Atlantic at the most eastern part of the English Channel and the Flemish Sea, from which it is evident that the arrival of the majority seems to take place in the beginning of the month of February. Thus, with the young-fish trawl off Cape Griz-Nez Gilson on the 6th and 7th of February took very large quantities of pelagic glass-eels of Stage 5, e. g. 100 and 175 per haul, which clearly shows that very large quantities occurred there at the time. (I may remark that the time for the arrival of the glass-eels found by Gilson is apparently in full

[1] I take this opportunity to make a remark with regard to my former statement (1906, p. 178) as to the speed at which the eel larvae move, because my former words on this matter have been a little misunderstood in a review of my work. I did not intend to say that the eel larvae in the first stages are slow in their movements, but only that they are slower than in the last developmental stages (4th—5th) which are greatly reduced in height. In reality the larvae often move at a great speed through the water, where like true eels they can advance and "go astern", the latter by undulating the compressed high body in the opposite direction.

agreement with the time for their ascent at the places nearer the Atlantic on the coasts of France and the British Isles; see Pl. XII in my paper of 1906).

From the Danish side a very large material of pelagic glass-eels has been collected, in addition to what has been mentioned in my 1906 paper, especially through Dr. A. C. Johansen's investigations with the "Thor". From these it appears that pelagic glass-eels occur in quantities in the salter parts of the Danish waters in the months of March and April (partly also in May). In 1907 they were for the first time found in Danish waters on the 28th of February by fisherman P. Villumsen in the stomachs of cod from the deeper, northern part of the Sound; 3 glass-eels were found which were sent me for investigation and proved to be in the 5th Stage A. When the glass-eels already so early as in February have been able to reach the Sound, I should be inclined to suppose that we have to do with specimens which have come into the North Sea north of Scotland and not through the English Channel, for the easterly migration of the glass-eels passing north of Scotland is not only shorter but is certainly also hastened to a much greater extent by the strong easterly current running there, which in autumn carries enormous quantities of Atlantic pelagic organisms into the North Sea (see Johs. Schmidt: The distribution of the pelagic fry and the spawning regions of the Gadoids in the North Atlantic from Iceland to Spain, 1908, p. 159 and Fig. 15). How great must be the importance of this current north of the British Isles to a merely passive transport of the eel-fry is for example seen by the "Goldseeker's" discovery of a larva in Stage 1 N. of Scotland on July 6th 1906 (59° 41′ N., 6° 00′ W., Depth: 230 m.) and by Helland-Hansen's discovery of a larva in Stage 3 (mentioned p. 14) near Bergen in Norway in October 1907. As mentioned in my paper above cited on the gadoid-fry, p. 162, the passive transport of pelagic organisms that takes place through the English Channel cannot in any way be compared in extent with the transport north of Scotland.

A systematic investigation as to the time at which the majority of the glass-eels pass north of the British Isles, as made from the side of Belgium in the English Channel, is therefore greatly wanted, for a closer study of this migration would be of fundamental importance to the solution of the question: how many of the Baltic eels originate from the sea W. of Scotland compared with those coming in through the English Channel from the spawning-grounds lying off the latter. Without entering into details I may give a short summary of the investigations of the occurrence of the pelagic glass-eels made from the "Thor" in the spring of the years 1906—08. In March and in the beginning of April Dr. A. C. Johansen found them in quantities at several places in the salter parts of the Danish waters outside as well as inside the Skaw. I also found them at several places in the central part of the North Sea during the last half of April 1906. But though they were specially searched for by numerous hauls I could not find a single specimen in the English Channel in the last days of April 1906, from which I may draw the conclusion that the majority of the glass-eels migrating from the Atlantic had then already passed this water (cf. Gilson's discoveries of large quantities of glass-eels in the beginning of February, as mentioned on p. 15). Neither in the Bay of Biscay nor in the waters near Ireland were glass-eels found in the months of May, though numbers of hauls were made (as to the only exception see p. 11).

All this indicates that the waters W. of the North Sea are after the month of April practically empty of pelagic glass-eels.

I may also just mention a couple of specially interesting observations regarding the migration of the glass-eels. At Valencia Island, Co. Kerry in south-west Ireland, the Misses Delap at my request kindly made some observations as to the time for the arrival of the glass-eels. It proved from these that the first specimens were found on November 20th (1907) after they had been searched for in vain at the end of October and in the beginning of November. By studying Pl. XII in my eel-paper of 1906, it will be seen that this locality (close by Castlemaine) is one of the places in Northern Europe which lies nearest to the 1000 m. curve, outside which the larvae in fact are found, and thus the arrival of the glass-eels

here so early as in November is quite comprehensible. It is however worth observing that according to the investigations of the Misses DELAP there are as yet only few glass-eels to be found in November and not until the following months do they occur in quantities.

Lastly, I may mention a very interesting discovery of a pelagic glass-eel (5th Stage) in waters in which this developmental stage had not previously been observed, namely, in the Baltic E. of Bornholm, where on May 4th 1908 it was taken by Dr. A. C. JOHANSEN from the "Thor". This specimen was only faintly pigmented. The exact locality was 54° 58′ N., 15° 41′ E. in the so-called Bornholm Deep. On his investigations with the "Thor" Dr. A. C. JOHANSEN has also at a few other places in the Baltic but W. of Bornholm[1] taken pelagic glass-eels but always only few, never in such numbers as in the salter parts of the Danish waters (North Sea, the Skager Rak, the Kattegat and the northern, deeper part of the Sound). Even though these later Danish investigations have drawn the limit for the occurrence of the pelagic transparent elvers somewhat further to the east, they however fully confirm the fact previously stated that the elvers greatly decrease in number to the east, i. e. in the direction away from the open sea.

[1] At St. 1210, May 1st 1908, S E. of Møen (54° 56′ N., 12° 42′ E): 1 specimen at a depth of ca. 50 meters.
- - 914, March 26th 1907, S. E. of Møen: 1 specimen at a depth of ca. 18 meters.
- - 905, March 23rd 1907, Fehmarn Belt: 3 specimens at the surface.
- - 902, March 22nd 1907, Langeland Belt: 2 specimens at the surface.

550. 24/II 1909.